

INTRASPECIFIC VARIATION IN POLLEN-OVULE RATIOS AND NECTAR SECRETION—PRELIMINARY EVIDENCE OF ECOTYPIC ADAPTATION¹

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ABSTRACT

Because pollen-ovule ratios (P/O's) reflect the predictability of pollinators in a habitat and the efficiency of pollination, large intraspecific differences in P/O's suggest differences in pollinator numbers and/or their efficiency. Plants of *Heracleum lanatum*, which is andromonoecious, from forests have larger percentages of male flowers than those outside of forests, hence a higher P/O. This difference is associated with differences in the kinds of flower visitors. I suggest the pollen removal by small bees that forage on *Heracleum* in but not outside the woods may be the selective force that accounts for the larger percentage of male flowers of woods plants.

In andromonoecious *Caesalpinia* the percentage of hermaphroditic flowers in a population ranges from 8–83%, and appears to be ecotypically adapted to levels of pollinator, i.e., butterfly, activity. Nectar secretion is continuous and is the key to successful reproduction, especially in populations with low pollinator activity. Pollination is proportional to foraging time and a function of the pollen carried. The amount of nectar in the flowers reflects pollinator activity; thus in low activity populations there will be more nectar and visits will be longer, thus increasing the likelihood of pollination. Because there are large numbers of male flowers in such populations the pollinators presumably carry more pollen, which also increases the likelihood of pollination. In populations with high pollinator activity large numbers of visits balance the shortness of individual visits. A consequence of this balanced system is that the fecundity of hermaphroditic flowers in quite dissimilar populations is equivalent. Deviations from predicted levels of seed set and fruit set are consistent with below normal levels of pollinator activity.

Nectar production in two populations of *Calliandra anomala* are quite different, with a high elevation population producing far less nectar than a lower elevation population. The low rate of nectar production in the high elevation population is undoubtedly an adaptation that forces the pollinators, i.e., hawkmoths, to visit large numbers of flowers to obtain sufficient nutrients, thus increasing fruit set and maximizing fecundity.

The breeding system and pollination biology of *Leonotis nepetaefolia* are used to explain the distribution of this African plant in Mexico, where it is a roadside weed.

The objective of this paper is to communicate initial results that suggest that two reproductive characteristics, "pollen-ovule ratios" and "nectar secretion," may have adapted ecotypically in response to differences in the kinds and levels of activity of their pollinators. Some of the data is of a preliminary nature, i.e., one year's observations, and in the future the present interpretation may require modification or reinterpretation.

FLORAL CHARACTERISTICS REVIEWED

For at least 15 years botanists have known that xenogamous flowers reflect reciprocal evolution with a pollinator class (Pijl, 1960, 1961). Floral morphology reflects the size and foraging behavior of the pollinator class. Flower color and odor reflect the visual and olfactory sensitivity of the pollinator class. For exam-

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ple, hummingbird flowers are typically red, have a tubular corolla with no "landing platform" or nectar guides, and produce no odor. In contrast bee flowers are typically blue, yellow, or white, frequently reflect ultraviolet light, may produce an odor, and have nectar guides and a "landing platform" that facilitates the landing of the insect on the flower. Recall also the rotten odor of carrion-fly pollinated flowers, e.g., *Stapelia*.

To the morphological characteristics we can add the constituents of nectar, e.g., amino acids and lipids, the timing of nectar secretion, and the quantity of nectar produced. For example, the nectars of butterfly flowers contain relatively large quantities of amino acids whereas the nectars of bee flowers contain relatively small quantities of amino acids (Baker & Baker, 1973, 1975). Bees have alternative sources of amino acids. Not surprisingly, carrion-fly flower nectars contain extremely high quantities of amino acids which help to simulate the usual microhabitat of the flies (Baker & Baker, 1973). With respect to the timing of nectar production, in *Penstemon kunthii* G. Don secretion begins approximately 1½ hours prior to the first visits by hummingbirds and ceases at approximately the same time the hummingbirds cease activity (Cruden et al., 1976). Further, the volumes and quantities of sugar in nectars reflect the energetic demands of the flowers' pollinators (Table 6). Thus it seems that virtually every aspect of the structure and function of xenogamous flowers is the result of co-evolution with their pollinators.

Characteristics of autogamous flowers reflect their breeding system. In comparing xenogamous and autogamous flowers Ornduff (1969) calls attention to a number of characteristics that facilitate self-pollination, e.g., introrse anthers that are adjacent to the stigma, as well as other characteristics that typify autogamous plants, e.g., small flowers and relatively low numbers of pollen grains. Such differences occur between species (Arroyo, 1973; Baker, 1967) and within species (Lloyd, 1965). As systematists we need to be aware that comparisons of floral characters may lead to erroneous phylogenetic conclusions if we unwittingly compare the products of convergent evolution. For example, in *Limnanthes* the utilization of floral characters led to taxonomic conclusions contrary to those generally accepted (Ornduff & Crovello, 1968). However, using vegetative characteristics the species fell nicely into two subgenera that represent two phyletic lines. In each phyletic line there is a series of species which include xenogamous species at one extreme and autogamous species at the other (Ornduff & Crovello, 1968).

A characteristic sometimes overlooked by systematists is the number of flowers that are open at a given time. Low numbers of open flowers maximize outcrossing in all plants and maximize effective pollinations in self-incompatible plants. Levin et al. (1971) suggested that the amount of legitimate pollen transfer decreases with each flower visited and that six to ten flowers is the maximum number of flowers that can be visited before all pollinations become geitonogamous. In *Calliandra*, fruit set ranged from 10–14% in those species and populations with few flowers open at a time compared to 1–5% in populations with many flowers open at a time (Cruden, 1976a).

TABLE 1. Relationship between pollen-ovule ratios, breeding systems, and successional stage.

Pollen-Ovule Ratio x̄ of x̄'s ± S.E.	Number of Popu- lations	Breeding System	Successional Stage	Number of Populations	Pollen-Ovule Ratio x̄ of x̄'s ± S.E.
27.7 ± 3.1	7	Obligate autogamy			
			Highly disturbed	23	135.6 ± 23.5
168.5 ± 22.1	20	Facultative autogamy			
			Early successional	24	588.7 ± 100.3
796.6 ± 87.7	38	Facultative xenogamy			
			Late successional Pollinators unreliable	23	1877.4 ± 423.6
5859.2 ± 936.5	25	Xenogamy	Late successional Pollinators reliable	15	7251.5 ± 1396.1

POLLEN-OVULE RATIOS

A pollen-ovule ratio (P/O) is the ratio of pollen grains produced per ovule. The details of calculating P/O's, a list of the species studied, etc. are presented elsewhere (Cruden, 1976b). P/O's range from 2.7 in cleistogamous flowers to over 1,000,000 in wind pollinated flowers. Using an outcrossing index, which was based on flower size, homogamy vs. dichogamy, and the relative position of stigmas and anthers, 96 populations representing 80 species were placed into one of several groups. Each group has a characteristic breeding system and P/O (Table 1). Obligately autogamous species have no apparent adaptations for outcrossing. Facultatively autogamous plants do have adaptations that facilitate outcrossing, but all those studied set full complements of seeds when pollinators were excluded. Many species produce nectar and are visited by potential pollinators, for example, *Verbena bracteata* Lag. & Rodr. and *Salvia tiliaefolia* Vahl, but outcrossing in this group probably is not the rule. Facultatively xenogamous plants are adapted for outcrossing, but all those studied were self-compatible and many were autogamous. Others required a pollinator. If dichogamous, they are protogynous, a system that favors outcrossing but does not preclude selfing. A good example of a facultatively autogamous species is *Mirabilis nyctaginea* (Michx.) MacMill., whose flowers open in late afternoon and are visited and pollinated by bees. They remain open during the night and are

TABLE 2. Breeding system characteristics and fecundity in *Hedeoma hispida*.

Population	1	2	3	4
Breeding System	Obligate Autogamy	Facultative Autogamy	Facultative Autogamy	Facultative Xenogamy
Length of flower/calyx	1	1.2	1.5	1.8
Width of corolla (mm)	1–1.5	2–3	2.5–3.5	3.4
Pollen-ovule ratio	39	64.2	109.9	244.7
Pollination (%)	100	100	98	43
Seed set (%)	98	97	93	73
Fecundity (%)	98	97	91	31

pollinated by moths; if unpollinated, they remain open and are visited again by bees in the morning, and if still unpollinated, they may self on closing (Cruden, 1973). Xenogamous species are outcrossers. Many, if not most, are self-incompatible. If self-compatible, they are probably strongly protandrous or more rarely functionally dioecious, as are many umbells (Cruden & Hermann-Parker, unpublished). Most species produce nectar and all those studied require a pollinator.

Prior to establishing the breeding systems of the species studied, each population was classified as to habitat or successional stage. It is not surprising that autogamous species are characteristic of highly disturbed habitats and that as succession occurs there is a switch to xenogamy. The data are consistent with accepted dogma, namely, that autogamy is adaptive in disturbed habitats because replication of successful genotypes assures continued success in such habitats. What is exciting and suprising is the ability to identify plants growing in advanced successional stages whose adaptations facilitate outcrossing but are able to self-pollinate or be selfed. If pollinators are unreliable, there is an obvious advantage in being self-compatible. The xenogamous plants in pollinator-unreliable habitats are, for the most part, early spring species, self-compatible, and protogynous. Xenogamous plants in habitats with reliable pollinators tend to be obligate outcrossers and suffer reduced fecundity if their pollinator activity is reduced (Cruden, 1972). The point is that breeding systems, including P/O's, are highly adapted to the ecological conditions in which the plant normally grows and in particular reflect the predictability of pollinators in the habitat.

Variation within species mirrors the variation that exists between species. Such differences were studied most thoroughly in *Hedeoma hispida* Pursh (Table 2). There is a significant increase in the P/O with the potential for outcrossing as measured by corolla exsertion and flower diameter. The increase in potential for outcrossing is correlated with a decrease in seed set in the autogamous populations, and there is a sharp decrease in both fruit set and seed set in the facultatively xenogamous population. The latter population was in a disturbed roadside park which lacked appropriate pollinators. It is clear that in disturbed habitats the facultatively xenogamous genotype would be at a selective disadvantage, with respect to reproductive success, compared to the autogamous genotypes. This illustrates the adaptive nature of autogamy in highly disturbed habitats, habitats in which pollinators may be absent or in low numbers.

VARIATION IN THE P/O'S OF ANDROMONOECIOUS SPECIES

A small number of plants produce inflorescences which contain both hermaphroditic and male flowers. Such inflorescences are typical of most Umbelliferae and some taxa in other families, e.g., various genera in Mimosaceae and Caesalpinaceae, and the commercially important *Mangifera indica* L. In four of five umbelliferous species studied to date the ratio of male to hermaphrodite flowers is constant. In *Heracleum lanatum* Michx. the ratio varies with habitat (Fig. 1). The number of hermaphrodite flowers in the primary umbells of "interior" plants is significantly different from those of plants in "openings" and outside the forest ($t = 3.94$; $p < .001$). Likewise the number of hermaphrodite flowers in the lateral umbells increases significantly from interior to outside populations ($F = 16.11$; $p_{df = 2, 69} < .001$). The array of flower visitors to inflorescences in "interior" populations is markedly different from that to "openings" and "outside" populations. The "interior" plants are visited heavily by small bees and small flies. The "outside" and "opening" plants are visited heavily by large flies and infrequently by small bees. The small bees may constitute a possible selective pressure if they remove significant amounts of pollen. In *Viola*, a small but significant decrease in the number of viable pollen grains was correlated with a significant decrease in fecundity (Cruden, 1976b). I suggest that increased numbers of male flowers may be a selective response to pollen loss from foraging bees. This hypothesis remains to be tested.

In *Caesalpinia* a number of reproductive parameters vary from population to population (Table 3), including percentage of hermaphroditic flowers, number of pollen grains per anther, and number of ovules. These three parameters contribute to the pollen-ovule ratio of a population and the P/O may vary markedly from population to population. The percentage of hermaphroditic flowers changes from year to year but probably varies around some genetically controlled mean. In other words, the variation we see probably has both a genetic and environmental component as is apparently the case in *Mangifera indica* (Free, 1970).

Data collected in 1975 (Table 4) suggest a positive correlation between the number of hermaphroditic flowers and butterfly activity ($r = .952$; $p = .05$). In those populations with low numbers of hermaphroditic flowers seed set is roughly proportional to pollinator activity. In the Mazatlán population seed set is low in spite of high pollinator activity. In general, fruit set is high when seed set is low.

A brief summary of pollinator behavior and the pollination biology of *Caesalpinia* will be helpful in understanding these results and the notions based on the results. The primary pollinators are species of *Battus* and *Papilio* (Papilionidae) which flutter before flowers while removing nectar. Pollen is carried on the underside of the wings and the wing area to stigmatic surface ratio is approximately 19,000:1, essentially equal to the bat-wing to stigma ratio of 18,000:1 reported for *Bauhinia pauletia* (Heithaus et al., 1974).

Although the ratio of male flowers is correlated with butterfly activity, the critical element in *Caesalpinia*'s reproductive biology is the continuous secre-

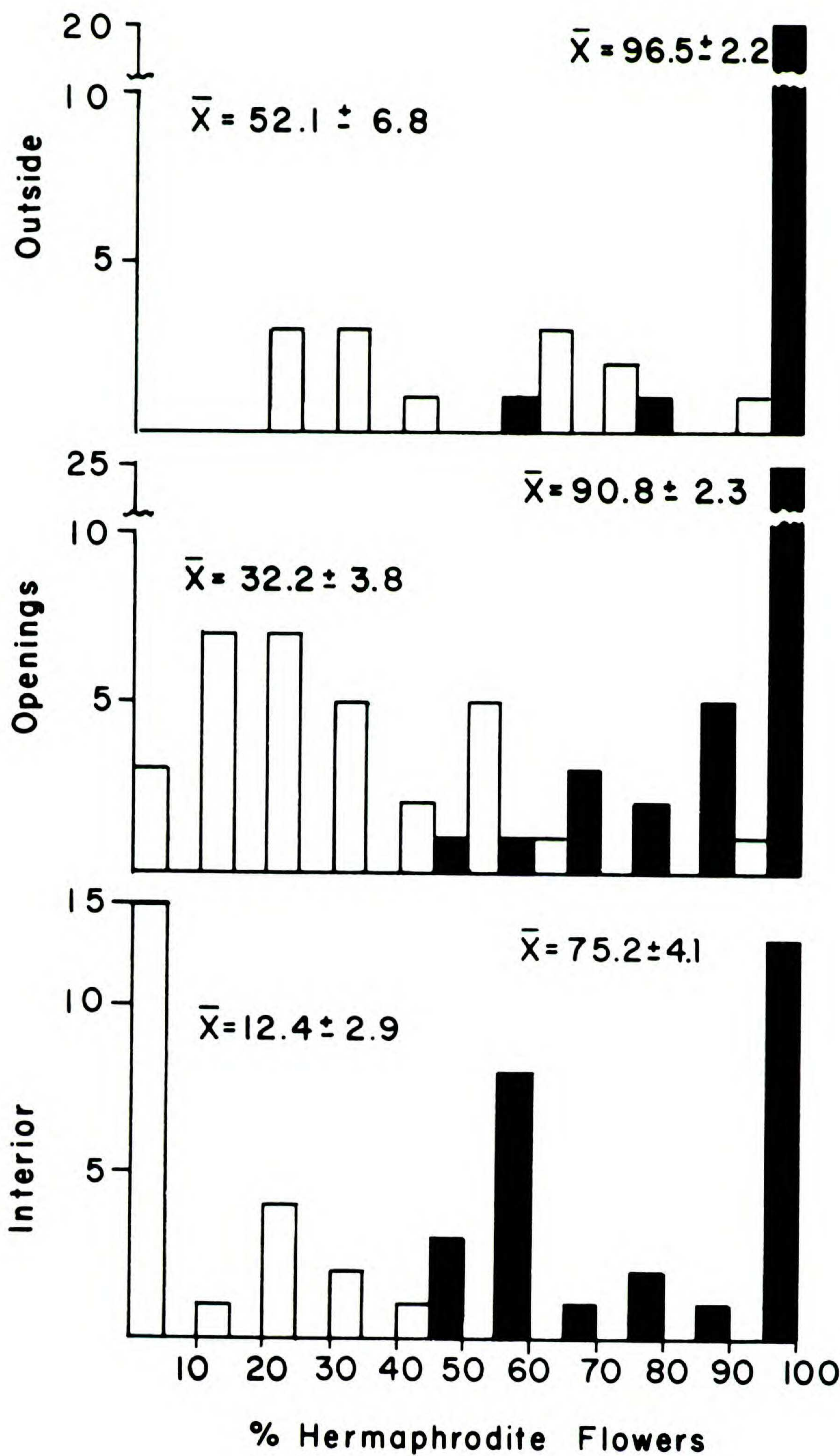


TABLE 3. Reproductive characteristics in four populations of *Caesalpinia pulcherrima* in Mexico.

	Year	Mazatlán	Colima NE	Miramar	Audiencia
Hermaphrodite flowers (%)	1974	83	23	14	—
	1975	88	33	27	11
Pollen grains per anther		721 ± 19	551 ± 53	606 ± 34	694 ± 23
Ovules per ovary		9.9 ± 0.2	6.2 ± 0.1	7.3 ± 0.1	6.7 ± 0.1
Pollen-ovule ratio	1975	877	3863	—	—
	1975	827	2693	3074	9416

tion of nectar. In other species for which we have data (N = 12) nectar accumulation reaches some maximum, and nectar secretion stops and resumes only if nectar is removed from the flower. The pattern of nectar secretion in *Caesalpinia* is thus atypical. The position and amount of nectar in male and hermaphroditic flowers also play an important role in the reproductive process. The rate of nectar secretion in hermaphroditic flowers is two to three times that in male flowers. The nectar in the male flowers is hidden deep in the floral tube which is a modified petal. The position and amount of nectar in male flowers serve to bring butterflies in contact with the anthers and little more. Nectar rises in the floral tube of the hermaphroditic flowers allowing a butterfly to hover higher thus increasing the likelihood of a butterfly's wing striking the stigma which is lateral to and higher than the anthers.

As the rate of nectar extraction is proportional to the amount of nectar in the flower, the butterflies spend more time at the hermaphroditic flowers. The greater the accumulation of nectar the greater the likelihood of successful pollen transfer.

The amount of nectar available to an individual butterfly is a function of the number of butterflies relative to the number of open flowers. If pollinator activity is high, little nectar is available and visits are short, but many flowers are visited. This should maximize fruit set and tend to result in lower seed set. Conversely, where pollinator activity is low, relatively large amounts of nectar will accumulate in the flowers and when a flower is visited, the butterfly will require more time to extract the nectar. Because fewer flowers are visited, fruit set should be lower but seed set will be high because of the increased pollen transfer that results from spending longer times at each flower. These predictions are consistent with our observations (Table 5).

These observations and assumptions suggest a testable hypothesis. First, if the percentage of male flowers in a population is a selective response to levels of pollinator activity, then large numbers of male flowers should act to increase

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FIGURE 1. Shift in the frequency of hermaphroditic flowers from shaded to open habitats in *Heracleum lanatum*. Solid bar = terminal umbell; Open bar = lateral umbells. $\bar{x} \pm \text{S.E.}$ are given for each group. Interior = below canopy; Openings = areas along streams where canopy is not closed; Outside = edge of forest where influence of canopy is minimal.

TABLE 4. Relationship between pollinator activity, percent hermaphrodite flowers, and seed set in populations of *Caesalpinia pulcherrima* in Mexico in 1975.

	Mazatlán	Colima NE	Miramar	Audiencia
Number pollinator visits/hr. to each flower (0900–1230 hrs.)	16.50	1.43	0.79	0.21
Hermaphrodite flowers (%)	88	33	27	11
Seed set (%)	59 ± 10 ^a	84 ± 2	75 ± 3	69 ± 3

^a 1974 data, 1975 seed crop destroyed by hurricane Olivia.

the pollen load carried by individual butterflies such that the total amount of pollen carried by the pollinator population is roughly equivalent in all populations. Second, because nectar secretion is continuous, relatively large amounts of nectar will accumulate in the flowers of “high male” populations. The likelihood of pollination will be increased because of large pollen loads and “long” visits at each flower. In “low male” populations equivalent levels of pollination may occur because the flowers are visited repeatedly. In essence, a stigma, regardless of the percentage of male flowers in the population, should be exposed to an equivalent number of pollen grains. This leads to the prediction that equivalent percentages of hermaphroditic flowers should set fruit in populations with quite different levels of pollinator activity, assuming the level of pollinator activity is equivalent to long-term levels of activity to which the flower population is adapted. Below normal levels of pollinator activity should result in decreased fruit set and increased seed set.

With respect to hermaphroditic flowers, fecundities in four populations (Table 5) were not equivalent. The fecundities of the Mazatlán and Audiencia populations were equivalent as were those of Colima NE and Miramar. The fecundities of the latter two populations are approximately 35% of the Mazatlán and Audiencia populations. The lower fecundities are the result of low fruit set. The low fruit set and the high seed set in these populations are consistent with the theoretical expectations for fecundity in populations with less than average pollinator activity.

TABLE 5. Relationship between percent hermaphrodite flowers, seed set, and fruit set in populations of *Caesalpinia pulcherrima* in Mexico.

	Year	Mazatlán	Colima NE	Miramar	Audiencia
Hermaphrodite flowers (%)	1974	83	23	14	—
	1975	88	33	27	11
Pollen-Ovule ratio	1974	871	3863	—	—
	1975	827	2693	3074	9416
Seed set (%)	1974	59 ± 10	68 ± 4	—	—
	1975	—	84 ± 2	75 ± 3	69 ± 3
Fruit set hermaphrodite/all flowers (%)	1974	15/13	10/2.3	—	—
	1975	—	5/1.7	4/1	14/1.5

TABLE 6. Mean nectar volumes and sugar concentrations in various flower classes.

Flower Class	Number of Species	Volume (μl)	Range	Sugar (mgm)	Range
Hawkmoth	20	31.67	3.83 –213.3	5.41	0.62 –26.3
Hummingbird	13	11.32	3.49 – 25.32	2.39	1.02 – 4.84
Butterfly	7	1.76	0.078– 3.96	0.43	0.024– 0.80
Bee	8	2.18	0.14 – 7.39	0.76	0.05 – 3.05

The equivalent fecundities in the Mazatlán and Audiencia populations are consistent with the model, i.e., that fecundities in hermaphroditic flowers should be equivalent in populations with quite different percentages of male flowers. For the moment, at least, I suggest that the number of male flowers in a population is an ecotypic response to levels of pollinator activity. However, it is the continuous nectar production that is the key to the system. Without continuous nectar production, fecundity in “high male” populations would be low due to short visits at each flower and reduced pollen transfer. Continuous nectar production through its effect on pollinator activity, especially in “high male” populations, effectively increases the likelihood of pollination.

NECTAR

Our work in nectar production (Cruden, Hermann-Parker & Peterson, 1976) has centered primarily on the differences between various flower classes. Our data substantiate the predictions of Heinrich & Raven (1972) and the field observations of numerous investigators that flowers pollinated by high energy requiring animals produce significantly more nectar than flowers pollinated by low energy requiring organisms (Table 6). Further, our studies show that the timing of nectar production is correlated with the activity cycle of the pollinator, as in *Penstemon kunthii* and in *Caesalpinia pulcherrima* Sw. In the latter species, nectar secretion starts approximately 30 minutes prior to the arrival of the first butterflies and nearly one hour before maximum butterfly activity.

Intraplant variation in nectar production plays an important role in the reproductive success of several plants we have studied, *Caesalpinia* being one example. For several decades (Epling & Lewis, 1952) botanists have known that bumblebees forage on *Delphinium* inflorescences from bottom to top. Steve Peterson, a graduate student at the University of Colorado, has found that the lower “pistillate” flowers produce twice as much nectar as the upper “staminate” flowers. The pattern of pollinator activity, undoubtedly a response to the amounts of nectar in the flowers, maximizes outcrossing in this self-compatible group.

Deceit has been implicated in the pollination of several species. Such may be the case in hummingbird pollinated *Cuphea llavea* Lav. & Lex, whose flowers mature acropetally as in *Delphinium*. The nectar of the “staminate” flowers contains $2.50 \pm .68$ mgm sugar compared to $.53 \pm .19$ mgm sugar in the “pistillate” flowers. The low amounts of nectar in the “pistillate” flowers and lack of nectar in approximately one-half of the flowers sampled suggest that nectar secretion

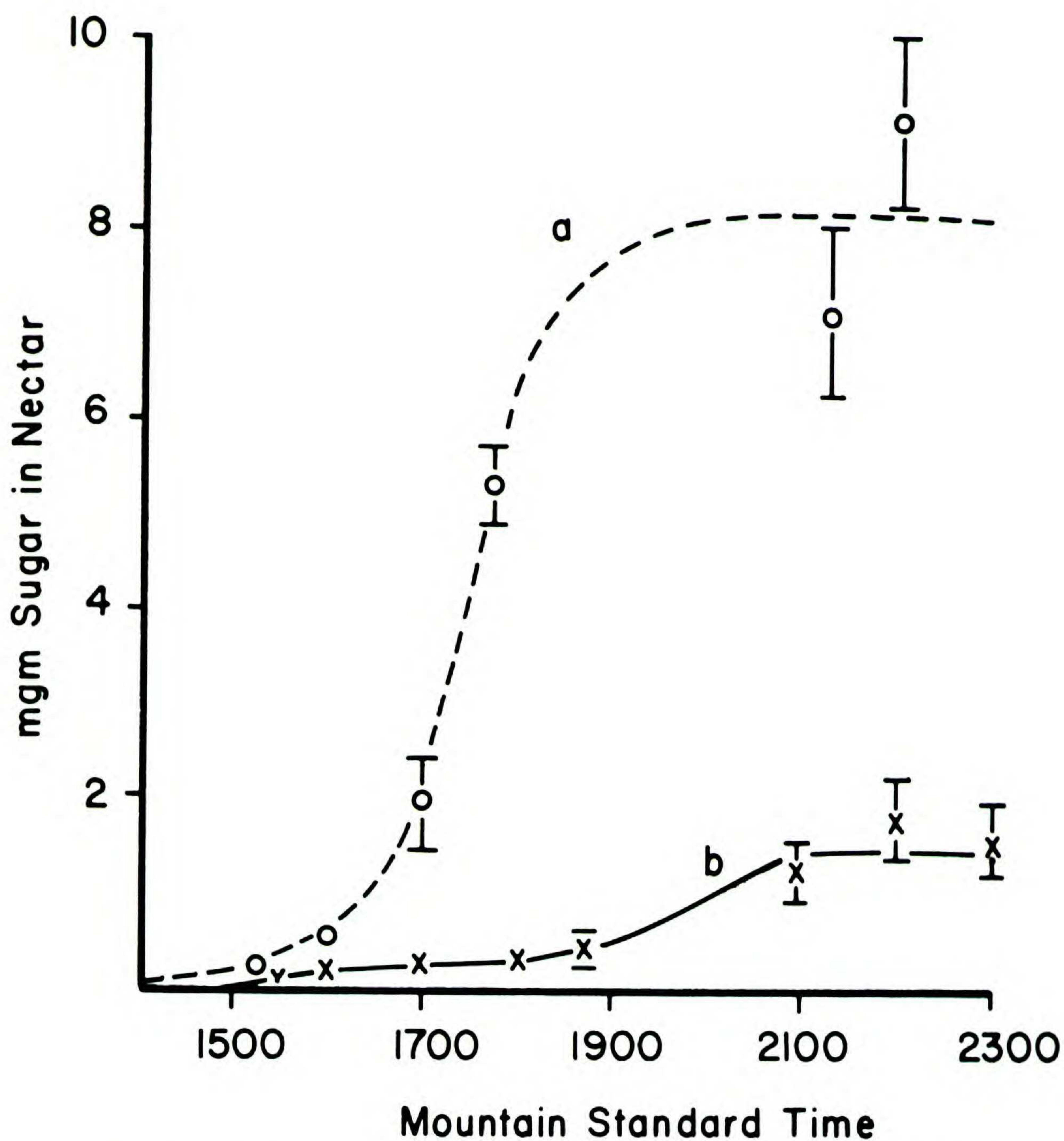


FIGURE 2. Nectar production in a 2,350 m population (solid line) and a 2,050 m population (broken line) of *Calliandra anomala*.

ceases after the “staminate” phase. By receiving a relatively large reward from the “staminate” flowers and occasional rewards from the “pistillate” flowers, the hummingbirds are not discouraged from visiting both staminate and pistillate flowers.

Our work on interpopulational differences in nectar production is somewhat meager, but the data generate tantalizing notions. We have studied nectar production in two populations of *Calliandra anomala* (Kunth) Macbr. (Fig. 2). The low elevation population is directly adjacent to the toll road from Mexico to Cuernavaca, probably resulting in severely reduced pollinator activity due to the constant movement of traffic. We studied a population at the same elevation a few kilometers away with respect to seed and fruit set (Table 7). Nectar

TABLE 7. Comparison of pollinator activity and reproductive success in two populations of *Calliandra anomala*.

	Low Elevation (2,100 m)	High Elevation (2,350 m)
Flowers visited (%)	42	78/49 ^a
Flowers pollinated (%)	25	18/11
Fruit set (%)	12	1
Seed set (%)	70	42
Fecundity	0.084	0.004

^a Two days' data.

production in this population is undoubtedly similar to that of the toll road population. Low nectar production in the high elevation population was correlated with larger numbers of visited flowers and lower numbers of pollinated flowers than the lower elevation population. Fecundity is clearly different.

At high elevations hawkmoths are active for brief periods of time. I have suggested elsewhere (Cruden, 1976a; Cruden et al., 1976) that low nectar production is an adaptation that maximizes fruit set by forcing the pollinator to visit large numbers of flowers. Fecundity is maximized because the first visit to a flower results in more seed set than subsequent visits. The adaptiveness of low nectar production in the high elevation *Calliandra* population is consistent with other hawkmoth pollinated species at high elevations. High elevation species regularly produce less than 1 mgm of sugar per flower ($\bar{X} = .99$, $N = 5$) compared to a mean of 5.66 mgm for 15 hawkmoth pollinated species studied at elevations below 2,400 m.

A second example of interpopulational differences in nectar production stimulates ideas as to the steps involved in the evolution of hummingbird flowers. Throughout most of its range the flowers of *Cuphea aequipetala* Cav. are small and probably produce small amounts of nectar as does a population at 3,000 m in the state of Morelos ($.48 \pm .05$ mgm sugar). This is consistent with the amount of sugar in the nectars of other bee pollinated flowers. Infrequently, at relatively low elevations (2,100–2,300 m) we found populations of large-flowered plants. In one of these the flowers produced large volumes of nectar containing $3.05 \pm .50$ mgm of sugar, which is more sugar than most hummingbird nectar contains.

TABLE 8. Characteristics of Mexican *Leonotis nepetaefolia* populations.

	Low	Mid
Elevational range	1–1,000 m	1,000–2,200 m
Flower length	19– 25 mm	30– 43 mm
Volume of nectar	$5.62 \pm 0.27 \mu\text{l}$	$11.54 \pm 0.74 \mu\text{l}$
Amount of sugar	$0.90 \pm 0.05 \text{ mgm}$	$1.91 \pm 0.13 \text{ mgm}$
Pollen-Ovule ratio	2,653	12,575
Probable pollinators	Hummingbirds, small bees	Large bees
Breeding system	Facultatively xenogamous	Xenogamous
Seed set in greenhouse	95%	63%
Fruit set in greenhouse	100%	95%

Both in Oaxaca and Jalisco, hummingbirds, as well as bees, foraged for nectar on *C. aequipetala*. Increased flower size and the concomitant increase in nectar production is a logical first step in the shift from bee to hummingbird pollination.

EVOLUTION OF THE WEED *LEONOTIS NEPETAEFOLIA*

Our interest in nectar production and P/O's first interested us in *L. nepetaefolia* R. Br., an African species widely distributed in the New World. Our nectar measurements called attention to significant differences in flower size between low and mid elevation populations (Table 8). The small-flowered form, which occurs along both coasts of the New World, is similar to specimens collected along the west coast of Africa. The earliest specimens I have examined date from the second decade of the 1800's. In the New World the large-flowered form is found almost exclusively in the central highlands of Mexico, primarily between 1,500 and 2,000 m. These plants are virtually identical with collections from around Nairobi, Kenya, in east central Africa. A third form of *L. nepetaefolia* occurs in eastern Africa and has undoubtedly given rise to the weedy populations in India, Southeast Asia, Indonesia, Australia, etc.

The small-flowered form is a good example of a facultatively xenogamous plant. It is visited and undoubtedly pollinated by hummingbirds and small bees. In the greenhouse, with bees excluded, fecundity was 98%. In contrast, the large-flowered form, which is pollinated by sunbirds in Kenya (Gill & Wolf, 1975), is visited illegitimately by hummingbirds which take nectar from the flowers by slitting the corolla or depressing it from above. The P/O (2,653:1) of the small-flowered form is consistent with its being facultatively xenogamous. The high P/O of the large-flowered race suggests xenogamy and is somewhat inconsistent with the relatively high level of fecundity (60%) in plants growing in the greenhouse. I suggest that the large-flowered form is recently arrived in the New World and that the evolution of an autogamous race may be occurring. The earliest specimens I have examined were collected in the 1930's. It is not unreasonable to suppose that the large-flowered form is an escape from horticulture and certainly any tendency toward autogamy would be rapidly selected. Indeed, if the African plants are not autogamous, escape from horticulture would be dependent on a mutation that permitted some selfing.

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